# A SYSTEMATIC AND PHYTOGEOGRAPHIC STUDY OF *ANTENNARIA AROMATICA* AND *A. DENSIFOLIA* (ASTERACEAE: INULEAE) IN THE WESTERN NORTH AMERICAN CORDILLERA

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## Abstract

*Antennaria aromatica* and *A. densifolia* are closely related species occurring in disjunct, unglaciated regions of the Rocky Mountain cordilleran system. The species are morphologically distinct and are readily distinguished based on a number of characters. They both occur on predominantly limestone talus slopes from subalpine to alpine elevations. Indications from the current distribution of the taxa and the known extent of glaciation suggest that they once had more extensive ranges and that these were subsequently reduced by the Wisconsinan glaciation. Glaciation has played a major role in the phytogeographic history of the species, as well as in their evolutionary divergence. A population of *A. densifolia* from Montana, disjunct from the main group of populations in the Northwest Territories and Yukon, is a noteworthy collection.

*Antennaria aromatica* Evert and *A. densifolia* A. Pors. are two narrowly restricted endemics of the Alpinae, a group of arctic/alpine *Antennaria* centered in western North America. Both occur on talus, primarily of limestone origin, but in different regions of the western North American cordillera. *Antennaria densifolia,* first described from the MacKenzie Mountains of the Northwest Territories, is apparently most common on the east slope of the MacKenzie Mountains and in the Ogilvie Mountains and southern Richardson Mountains of the Northwest Territories and Yukon Territory. Evert (1984) recently described *A. aromatica* from the Rockies of Montana and Wyoming (type from the Beartooth Pass near Quad Creek, Montana). Examination of herbarium material and the meager literature indicates that the morphological, ecological and distributional aspects of these two species are not well understood. Distributions of the species indicate that they once may have been more widespread and that their phytogeographic history, as well as their evolutionary divergence, was influenced greatly by Pleistocene glaciation. Comparison of specimens of both species indicates a close morphological similarity. Recently, a single disjunct population of *A. densifolia* has been discovered in a remote area of Montana. This, coupled with the ostensible morphological and ecological similarity of the two species, makes a detailed analysis of them appropriate.

TABLE 1.   LIST OF 36 CHARACTERS AND CHARACTER STATES USED IN THE MORPHO-METRIC ANALYSIS OF *ANTENNARIA AROMATICA* AND *A. DENSIFOLIA*. Numbers following each character indicate the scale used. All qualitative state determinations are in mm.

Basal rosette characters: 1. Length of entire basal leaf. 2. Maximum width of the basal leaves. 3. Length, along the mid-vein, from leaf tip to the maximum width. 4. Shape of the anterior margin, i.e., length from tip to widest point in the leaf. 5. Number of leaves per basal rosette.

Stolon characters: 6. Number of leaves per stolon. 7. Length of the largest leaf. 8. Width of the largest leaf. 9. Length of the smallest leaf. 10. Width of the smallest leaf. 11. Stolon length. 12. Number of stolons per basal rosette.

Cauline (flowering) stem characters: 13. Flowering stem height. 14. Number of leaf nodes per cauline stem. 15. Width of the longest leaf. 16. Length of the longest leaf. 17. Width of the shortest leaf. 18. Length of the shortest leaf. 19. Presence of a scarious flag-like structure at the apex of the upper leaves, 0.0 = absent, 1.0 = present.

Pistillate capitulescence characters: 20. Height of the involucre. 21. Number of heads per capitulescence. 22. Phyllary length. 23. Phyllary width. 24. Corolla length. 25. Pappus length. 26. Achene length. 27. Phyllary colors, 1.0 = green base, white tips, 2.0 = green base, rose middle, white tips, 3.0 = green base, black/brown middle, white tips, 4.0 = green base, brown middle, rose tips, 5.0 = green base, brownish tips, 6.0 = brown base, white tips, 7.0 = brown base, rose tips, 8.0 = brown base, umber tips, 9.0 = brown base, dark brown tips, 10.0 = brown base, black or very dark green tips. 28. Number of florets per head.

Staminate capitulescence characters: 29. Height of the involucre. 30. Number of heads per capitulescence. 31. Phyllary length. 32. Phyllary width. 33. Corolla length. 34. Pappus length.

Miscellaneous characters: 35. Presence of stalked glands on the surfaces of stems, leaves, etc., 0.0 = absent, 1.0 = present. 36. Presence of staminate individuals in the population, 0.0 = staminates absent (i.e., population all pistillate), 1.0 staminates present.

## METHODS

Specimens deposited at ALA, ALTA, CAN, DAO, ID, MONTU, RM, and UAC were examined for the morphological and phyto-geographic information. Chromosome counts were obtained from several collections of *A. aromatica* and one of *A. densifolia* utilizing the Feulgen chromosome staining methods described in Bayer (1984).

A principal components analysis (PCA) was used to quantify the morphological differences between the species. Forty specimens representing the range of morphological diversity from throughout the known range of each species were selected for morphometric analysis. Thirty-six vegetative and reproductive features (Table 1) were measured on twenty specimens of each taxon. In most cases specimens, having both staminate and pistillate individuals, were used, but complete specimens could not always be included because of the scarcity of good material. The original data matrix is available from the author upon request.

The NTSYS-pc program (Numerical taxonomy and multivariate analysis systems for the IBM-PC microcomputer and compatibles;

vers. 1.2; F. James Rohlf 1987) was used to compute the PCA. The STAND subroutine was used to standardize the data such that each character had a mean of zero and a standard deviation of unity. A similarity matrix of product-moment correlations was derived using the SIMINT subroutine of NTSYS-pc. The EIGEN subroutine was employed to compute the eigenvalue and eigenvector matrices. Three factors were extracted by the EIGEN subroutine. The OTU's were subsequently projected onto axes (the eigenvectors) using the PROJ subroutine of NTSYS-pc, thus concluding the principal components analysis. A 3-dimensional graph of the OTU's onto the first three principal components was plotted using the MOD3DG subroutine of NTSYS-pc.

## RESULTS

*Distribution and cytology.* The distribution of all available herbarium records for both taxa is presented in Figure 1. Additionally, the distribution of herbarium records having staminate, as well as pistillate specimens, and those having only pistillate specimens, is indicated. Although absence of staminate plants, as determined from gender ratios in natural populations, is a dependable indicator that the plants in the population are gametophytic apomicts (Bayer and Stebbins 1983), the lack of staminate plants on herbarium specimens provides only weak evidence because it could be a consequence of the failure of the collector to gather both genders in a particular population.

The base chromosome number in *Antennaria* is $x=14$. The only previous chromosome report (diploid) for *A. densifolia* is a Yukon population (Chmielewski and Chinnappa 1988). One population of *A. densifolia* from Montana has been determined as diploid (Table 2). Three populations of *A. aromatica* have been counted as diploid, whereas seven are tetraploid (Fig. 2, Table 2). One population of *A. aromatica* from the Big Horn Mountains has been counted as hexaploid, or $2n=84$ (Fig. 2, Table 2), which is a new number for the species. The three diploid populations of *A. aromatica,* including the type locality, are from the southern part of the species range (Fig. 2). The tetraploid populations are more widespread, occurring from

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FIG. 1. Distribution of *Antennaria aromatica* (circles) and *A. densifolia* (squares) in western North America (each symbol may depict one or more collections). Open symbols indicate collections containing pistillate and/or staminate individuals, while closed symbols signify collections having only pistillate plants. The continental divide is indicated by the dot/dash line and the Wisconsinan glacial maximum, following Prest (1984), is shown by "T" shaped symbols. Bar = 500 km.
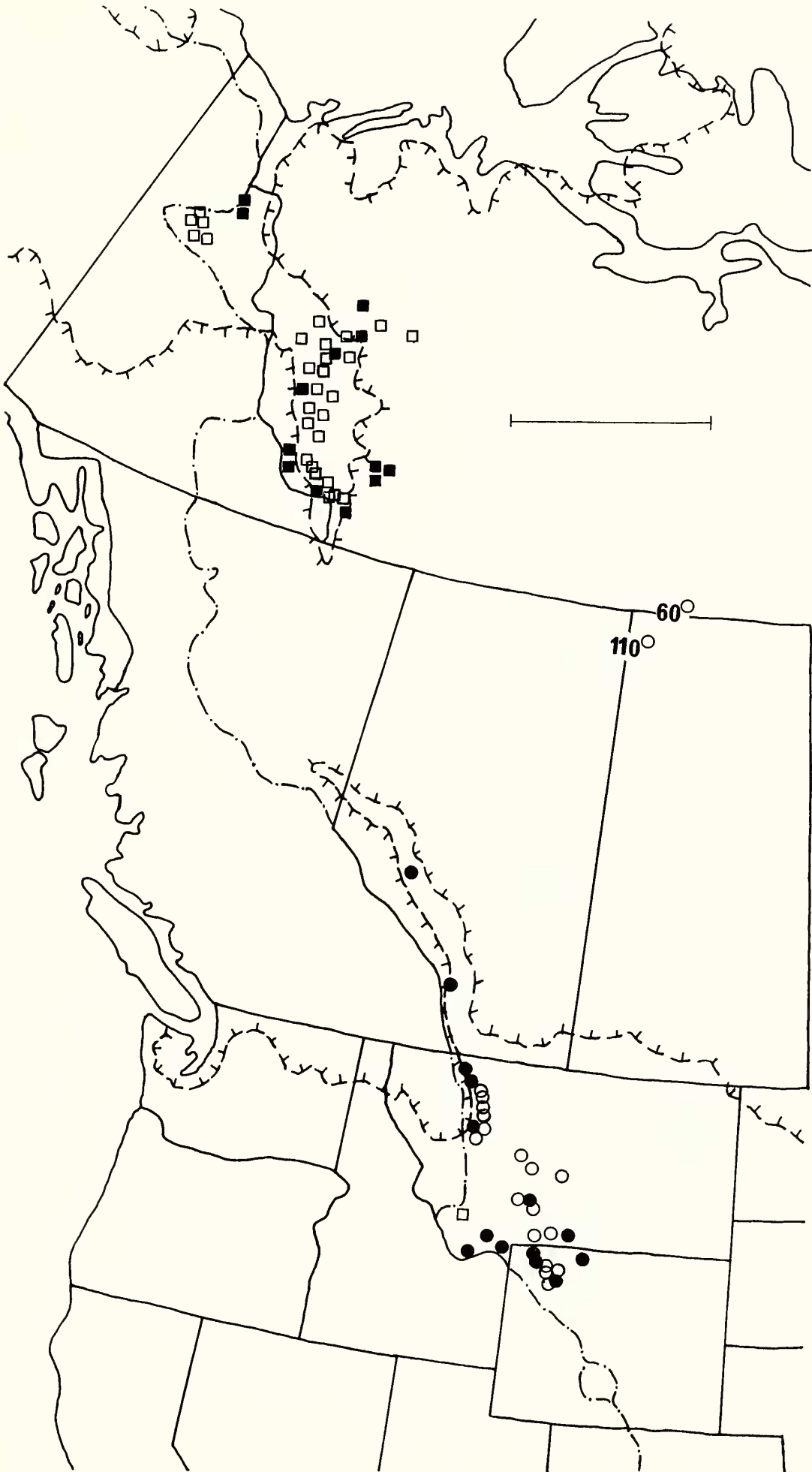
TABLE 2. SYNOPSIS OF CHROMOSOME NUMBERS FOR ELEVEN POPULATIONS OF *ANTENNARIA AROMATICA* AND TWO POPULATIONS OF *A. DENSIFOLIA*. Presented are state/ province, county or mountain range, and voucher number. Report reference codes: a = current study (vouchers at ALTA), b = Bayer (1984), c = Bayer and Stebbins (1987), and d = Chmeilewski and Chinnappa (1988). * = new number for the species. ** = population presumably asexual, containing only pistillate individuals.

| State or province | County or mountain range | Voucher number | Somatic number | Reference codes |
|---|---|---|---|---|
| *A. aromatica*: | | | | |
| Montana | Carbon Co. | 8092 | 28 | b |
| Montana | Gallatin Co. | MT-628 | 28 | a |
| Wyoming | Park Co. | WY-836 | 28 | a |
| Montana | Cascade Co. | MT-747 | 56 | a |
| Montana | Gallatin Co. | 8105** | 56 | b |
| Montana | Judith Basin Co. | MT-754 | 56 | a |
| Montana | Lewis and Clark Co. | MT-890 | 56 | a |
| Montana | Madison Co. | MT-634** | 56 | a |
| Montana | Teton Co. | M-302 | 56 | c |
| Wyoming | Park Co. | WY-626** | 56 | a |
| Wyoming | Big Horn Co. | WY-813** | 84* | a |
| *A. densifolia*: | | | | |
| Montana | Granite Co. | MT-725 | 28 | a |
| Yukon | Ogilvie Mtns. | 2642/2643 | 28 | d |

the northern part of the range in Teton Co., Montana south to Madison Co., Montana and Park Co., Wyoming (Fig. 2).

*Morphometrics.* The 3-dimensional graph displaying the first three factors from the principal components analysis (PCA) is presented as Figure 3. The first three axes account for 57.06% of the variation and the first 10 factors have individual eigenvalues greater than 1.000, indicating that the variables are not highly correlated. Factor 1 has highest loadings for the characters of presence/absence of glands (Table 1; character 35), pistillate phyllary length (character 22); and various leaf length characters (characters 1, 7, and 9). Stolon length (character 11), number of stolons/basal rosette (character 12), and the presence/absence of staminate clones (character 36) have high loadings in factor 2. Factor 3 has high loadings for staminate corolla length (character 33) and length of the basal rosette leaves (character 1). *Antennaria aromatica* and *A. densifolia* form two distinct groups (Fig. 3) and disassociate best along factor 1. The diploid and tetraploid cytotypes of *A. aromatica* appear to form two groupings along factor 2. A trend toward the separation of sexual and asexual populations of *A. aromatica,* as expressed by presence/absence of staminate plants, is evident on factor 2. Although two
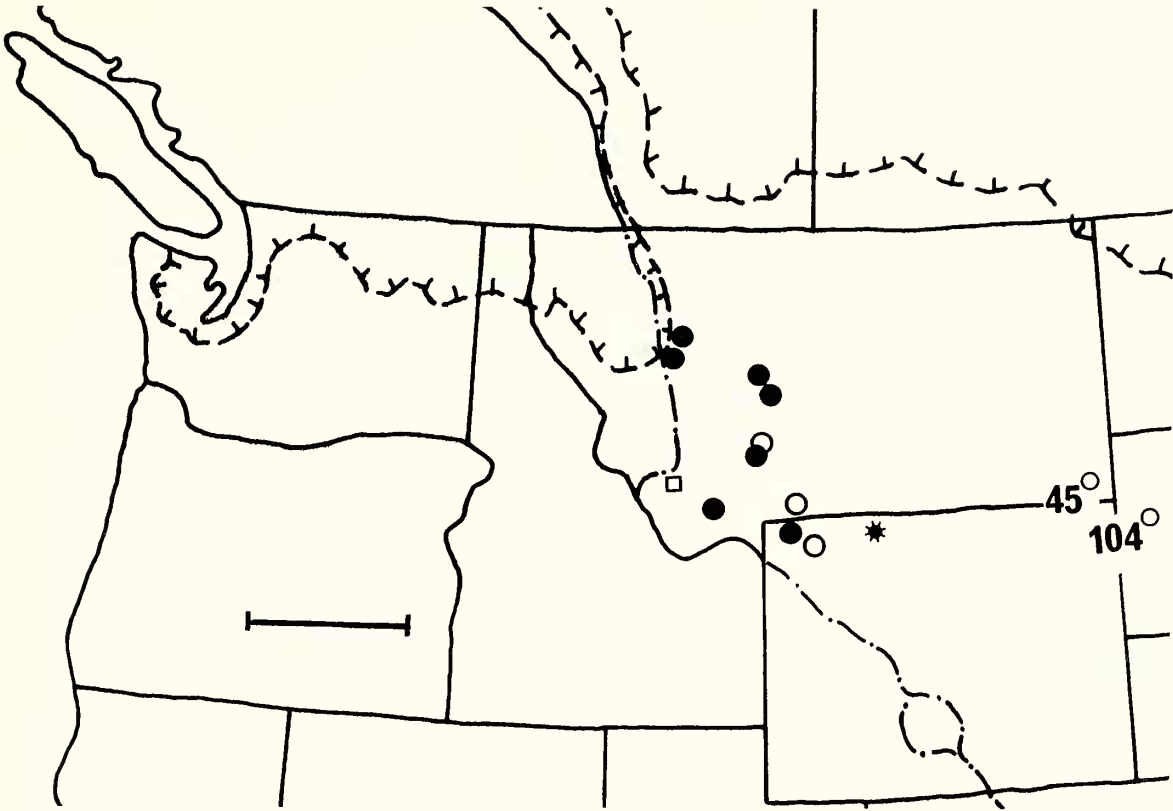
FIG. 2.    Distribution of cytotypes of *Antennaria aromatica* and *A. densifolia* in Montana and Wyoming. Open circles = diploid, closed circles = tetraploid, and star = hexaploid populations of *A. aromatica*. The open square is a diploid population of *A. densifolia*. The continental divide is indicated by the dot/dash line and the Wisconsinan glacial maximum, following Prest (1984), is shown by "T" shaped symbols. Bar = 250 km.

subgrouping are apparent within the *A. densifolia* cluster (Fig. 3), it is not certain whether these two represent different ploidy levels.

## DISCUSSION

The direct relationship of *A. aromatica* to *A. densifolia* is indicated by similarity of morphology and ecology. They are part of a larger complex of arctic/alpine *Antennaria* (Alpinae group) and consequently are related to *A. umbrinella* Rydb. and *A. pulchella* E. Greene (Bayer 1987b). Using a taxonomic species concept, *A. aromatica* and *A. densifolia* can be considered discrete species because they are morphologically distinct. The PCA demonstrates this conclusively, and indicates that the presence of stalked glands (and the coincident citronella odor in the living plants) in *A. aromatica* and the complete lack of these glands in *A. densifolia* distinguishes them reliably. Three other characters can be used to separate the two species. Most individuals of *A. densifolia* possess flat, scarious, linear-lanceolate tips, termed "flags", at the ends of the upper cauline leaves (character 18; Table 1), however most *A. aromatica* lack these flags. The basal
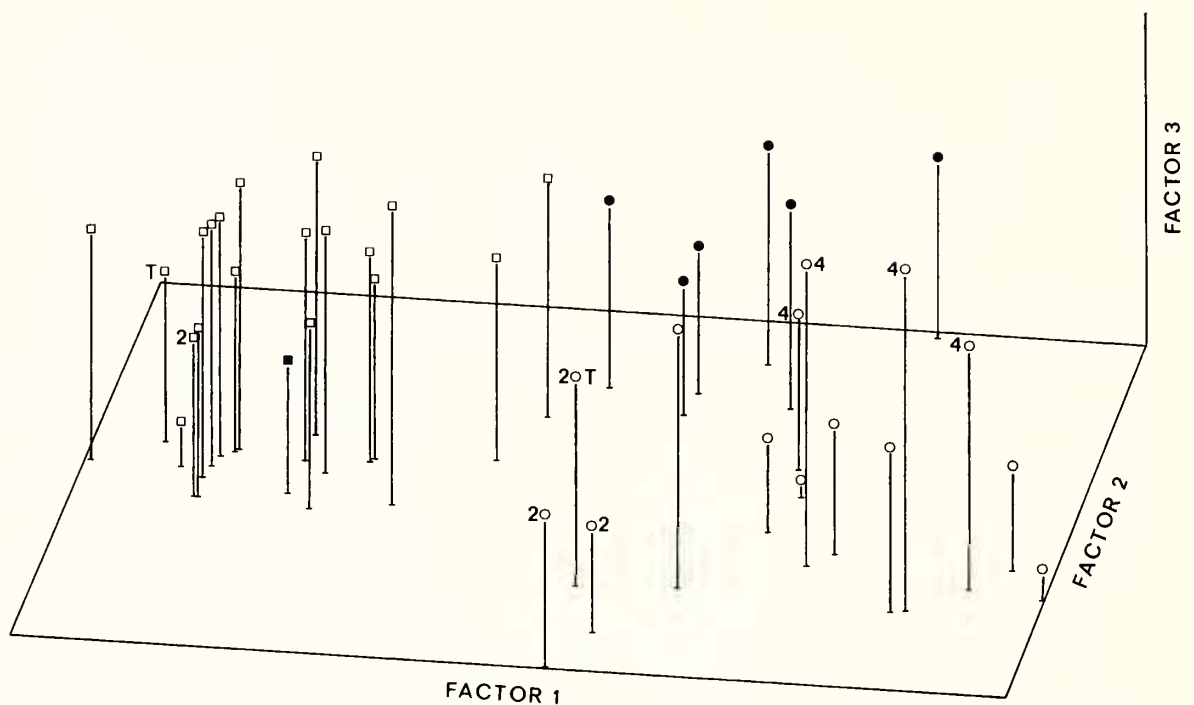
Fig. 3. PCA composed of 20 OTU's of *Antennaria aromatica* (circles) and 20 of *A. densifolia* (squares). Open symbols indicate collections containing pistillate and/or staminate individuals, whereas closed symbols signify collections having only pistillate plants. An isotype of *A. aromatica* (ALTA) and the holotype specimen of *A. densifolia* (CAN) are marked with "T". Specimens of known chromosome number are labeled "2" for diploid and "4" for tetraploid. The one disjunct diploid population of *A. densifolia* from Montana is the open square labeled "2".

rosette leaves (character 1) in *A. aromatica* are 6.0–16.0 mm long (mean 9.4 ± 2.9), whereas those of *A. densifolia* are 3.0–6.0(–7.0) mm long (mean 4.7 ± 1.1). *Antennaria aromatica* has pistillate phyllaries that are (4.0–)5.0–7.0 mm long (mean 5.6 ± 0.76) and those of *A. densifolia* are 3.0–5.0 mm long (mean 4.1 ± 0.58). These three characters are not as reliable as presence/absence of glands to separate the taxa, but the character suite is relatively reliable.

*Antennaria aromatica* was first described (Evert 1984) from the Beartooth Mountains of Montana, but has since been collected from several additional sites in Montana, Wyoming, and Alberta. The species is known only from ca. 40 collections (including several duplicate collecting efforts), but is perhaps more common within its rather restricted range than the scant herbarium record would indicate because of the relative inaccessibility of habitats where these plants are known to occur. Several older collections exist in herbaria, but they were not recognized as belonging to a new species. They are most often misidentified as *A. alpina* (L.) Gaertner, *A. media* E. Greene, or *A. umbrinella*.

Since the description of *A. aromatica*, there has been some confusion about its identity and geographic range. In 1898, Greene described *Antennaria pulvinata* from Moose Mountain in the Front

Range of the Rockies west of Calgary, Alberta (Bayer 1989). This taxon is entirely pistillate and resembles *A. aromatica* closely, except it lacks the glandular hairs. These apomicts are polyploids that undoubtedly have *A. aromatica* as one of their sexual progenitors, but probably have other sexual parents as well (Bayer in press a). I have included these apomicts, and others like them, in the *A. rosea* E. Greene polyploid complex, calling them *A. rosea* subsp. *pulvinata* (E. Greene) R. Bayer (Bayer 1989). Recently, Weber (1987) and Hartman and Rottman (1988) reported *A. aromatica* from Colorado, but I would instead identify these plants as *A. rosea* subsp. *pulvinata*.

Authentic *A. aromatica* is a cushion plant that occurs on talus slopes, almost always composed of limestone. The populations occur from just below treeline to alpine, but, in my experience, are often found just at the treeline with the krummholz vegetation. The plants are viscid, and the younger foliage has a strong citronella odor. The populations are usually sexual, having approximately equal proportions of staminate and pistillate clones (Fig. 1). Some of the common associates of *A. aromatica* are *Androsace chamaejasme, Anemone multifida, Aquilegia jonesii, Arctostaphylos uva-ursi, Arenaria obtusiloba, Astragalus gilviflorus, Astragalus kentrophyta, Cymopterus hendersonii, Draba oligosperma, Dryas octopetala, Eriogonum androsaceum, Eritrichium nanum, Haplopappus uniflorus, Hedysarum alpinum, Hulsea algida, Ivesia gordonii, Paronychia sessiliflora, Pedicularis parryi, Phlox caespitosa, Phlox hoodii, Physaria didymocarpa, Potentilla fruticosa, Ribes oxycanthoides, Valeriana edulis,* and *Zygadenus elegans.*

All populations of *A. aromatica* occur east of the continental divide, predominantly in areas that were unglaciated during the Wisconsinan (Fig. 1). *Antennaria aromatica* could be restricted to the Front Ranges east of the divide as a result of climatic factors, these mountains receiving less rainfall than those to the west in western Montana and eastern Idaho. The main range of the species is from north-central Wyoming, near Cody, north to Glacier National Park, Montana (Fig. 1). Two minimally disjunct populations of *A. aromatica* occur in the Alberta Rockies, which extends the range of the species to the Mountain Park area east of Jasper, Alberta (Fig. 1). These two collections (ALTA #27162 and #32291) are the first of this species from Canada. The collection from Mountain Park is especially significant because this is not only an area with large areas of limestone outcrops, but is an area that has been identified as a glacial refugium (Packer and Vitt 1974; Prest 1984) and is known for its large number of species disjunctions.

*Antennaria aromatica* occurs as both diploid and polyploid races (Table 2). The PCA demonstrates that the two groups (diploids and polyploids) are slightly distinct morphologically (Fig. 3). Although the two cytotypes cannot be reliably distinguished on morphological

grounds, the diploids are mostly smaller in all respects when compared to the polyploids (pistillate involucres in the 3 confirmed diploids are 5.0–6.0 mm high, whereas those of four tetraploids are (6.0–)6.5–7.5 mm high). Similarly to other species of *Antennaria*, populations of the *A. aromatica* diploid cytotypes have equal proportions of staminate and pistillate clones (Bayer unpubl. obs.). Some of the tetraploid populations have both staminate and pistillate plants, whereas others have only pistillate plants (Table 2, Fig. 2). The only known hexaploid population is entirely pistillate (Fig. 2, Table 2). *Antennaria aromatica* conforms to a pattern that appears in several other species of *Antennaria,* such as *A. marginata* and *A. media,* one in which populations of the diploid cytotype within a species are sexually reproducing. Populations of the polyploid cytotype, which are for the most part morphologically indistinguishable from the diploids, are either sexually or asexually reproducing. The diploids frequently have a much more restricted range than the polyploids and are often found strictly in unglaciated regions, whereas the polyploids have wide ranges in both glaciated and unglaciated areas (Bayer and Stebbins 1981). Asexual polyploids are also the ones that usually colonize the areas farthest away from the center of the species range and/or into glaciated terrain. The distribution of cytotypes within *A. aromatica* (Fig. 2) corresponds well to this pattern.

*Antennaria densifolia* was originally described by Porsild (1945) from the east slope of the MacKenzie Mountains, Northwest Territories. Porsild (1945) stated that it superficially resembled *A. pulvinata* E. Greene and *A. compacta* Malte. In Porsild's keys to species for arctic Canada (Porsild 1950; Porsild and Cody 1980), the means of distinguishing *A. compacta* from *A. densifolia* is by the lack of staminate individuals in *A. compacta,* and its longer, more linear, basal leaves.

The habitat of *A. densifolia* is similar to that of *A. aromatica*; i.e., calcareous talus, ranging from subalpine through treeline to alpine. Specimen data suggest that *A. densifolia* occurs most often in alpine situations, and *A. aromatica,* most often in the subalpine or at treeline.

In constructing the distribution maps of *A. densifolia,* I identified some specimens lacking staminate plants as *A. densifolia* although by using Porsild's key (Porsild 1950) they are *A. compacta.* These specimens have the shorter, cuneate leaves of *A. densifolia* and probably represent the disregard of staminate plants on the collectors' part. Most of these collections were made near other sites where staminates are known to occur (Fig. 1). About 40 populations containing both staminate and pistillate individuals are now confirmed, but many of these sites are very close together along the only roads in the areas, the Dempster highway over the Ogilvie and Richardson mountains and the north Canol road over the MacKenzie Mountains

(unfortunately, the road is now abandoned and impassable in the region where *A. densifolia* is known). The large number of specimens from the southern MacKenzie Mountains in the Nahanni National Park were probably collected during the initial vegetation surveys of this wilderness park. The distribution of *A. densifolia* (Fig. 1) is in two slightly disjunct areas, the eastern slopes of the MacKenzie Mountains, and the northern Ogilvie and southern Richardson mountains. Although *A. densifolia* has not been collected in the remote interlying region, the valley-glaciated Wernecke Mountains, it is possible that it does occur there because dolomitic limestone outcrops exist in this range (Oswald and Senyk 1977). The northern Ogilvies and southern Richardsons had only limited alpine glaciation during the Wisconsinan (Prest 1984). The eastern slope of the MacKenzies were part of the northern end of the western Canadian ice-free corridor (Rutter 1984), but perhaps had restricted alpine glaciers during the Wisconsinan. The majority of the *A. densifolia* populations containing staminate plants are located within the unglaciated regions, only three populations being located in previously glaciated terrain (Fig. 1).

One very noteworthy collection was our (*Bayer, DeLuca, and Lebedyk MT-725* at ALTA and RM or *Lackschewitz 4611* at MONTU) recent discovery of a population of *A. densifolia* in the Anaconda Range of Granite Co., Montana (Figs. 1 and 2) found growing in gravelly, limestone talus on open alpine tundra. This site represents not only the first collection of the species for the United States, but a substantial (1850 km) disjunction from the nearest population in the Northwest Territories. Morphologically the plants from Montana are well within the range of typical *A. densifolia* from Canada (Fig. 3) and are diploid, the same as the only available count for northern Canadian *A. densifolia* (Table 2).

Although only diploid counts have been obtained for *A. densifolia*, it is probable that some tetraploid populations exist, as two weakly distinct subgroups within *A. densifolia* are present in PCA (Fig. 3). It is possible that this species repeats the pattern of morphologically indistinguishable diploid and sexual polyploid races present within species. Additional chromosome counts are needed to confirm or reject this hypothesis. *Antennaria densifolia* is similar to *A. aromatica*, in that a group of apomicts (*A. compacta*) derived from *A. densifolia* are morphologically very similar to their parent. In a similar manner, there are polyploid apomicts related to *A. aromatica* (*A. rosea* subsp. *pulvinata*). The taxa can be identified by means of the following key.

KEY TO *ANTENNARIA AROMATICA, A. COMPACTA,* AND *A. DENSIFOLIA*

A   Basal leaves linear to linear-oblanceolate, two or more times longer than wide, arising from densely tufted basal caudices. .................... *A. compacta*

A′  Basal leaves cuneate to cuneate-spathulate, less than two times longer than wide, densely caespitose and arising from short, prostrate stolons.
  B  Stalked glands present on flowering stalks, phyllaries, and leaves; odor of citronella present in living plants; flags usually lacking from upper cauline leaves, basal leaves mostly 6.0 mm or more long; pistillate phyllaries mostly 5.0 mm or more long. ..................................... *A. aromatica*
  B′  Stalked glands absent from flowering stalks, phyllaries, and leaves; living plants odorless; flags usually present on upper cauline leaves; basal leaves mostly less than 6.0 mm long, pistillate phyllaries mostly less than 5.0 mm long. ..
  ................................................................. *A. densifolia*

The distributions of *A. aromatica* and *A. densifolia* (Fig. 1) provide clues to the phytogeographic and evolutionary history of the two species. It is probable that both species may once have had much wider ranges, and the advance of the Cordilleran and Laurentide ice sheets during the Wisconsinan obliterated the greater part of their former ranges. Sexual dioecism evidently prevents swift migration, as few sexual species of *Antennaria* have extensive ranges in glaciated terrain (Bayer and Stebbins 1987). The solitary population of *A. densifolia* in Montana near the southern end of the ice-free corridor (Fig. 1) may indicate that the species once occurred more widely as far south as Montana and was eliminated from the intervening areas of British Columbia and Alberta. The main body of populations of *A. densifolia* remaining today are in the unglaciated area at the northern end of the corridor (Fig. 1). *Antennaria aromatica* exists at the southern end of the corridor, but the two Alberta populations (Fig. 1) that rest within the corridor itself indicate that the species may have once had a much larger range. The populations near the ice margin and within the ice-free corridor probably survived in situ, because, as pointed out by Packer and Vitt (1974), suitable habitats for other endemic calceophiles exist in the surrounding glaciated region, yet the species that are found within the refugial area in Mountain Park, Alberta have not migrated to them.

*Antennaria aromatica* and *A. densifolia* are obviously very closely related and it is probable that they evolved from the same common ancestor (Bayer in press b). Glaciation was probably the vicariant event that separated the series of populations, and the ensuing isolation perhaps facilitated further divergence.

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LITERATURE CITED

BAYER, R. J. 1984. Chromosome numbers and taxonomic notes for North American species of *Antennaria* (Asteraceae: Inuleae). Syst. Bot. 9:74–83.

————. 1987a. Evolution and phylogenetic relationships of the *Antennaria* (Asteraceae: Inuleae) polyploid agamic complexes. Biol. Zentralbl. 106:683–698.

————. 1987b. Morphometric analysis of western North American *Antennaria* Gaertner (Asteraceae: Inuleae). I. Sexual species of sections Alpinae, Dioicae, and Plantaginifoliae. Canad. J. Bot. 65:2389–2395.

————. 1989. A taxonomic revision of the *Antennaria rosea* (Asteraceae: Inuleae: Gnaphaliinae) polyploid complex. Brittonia 41:53–60.

————. In press a. Investigations into the evolutionary history of the *Antennaria rosea* (Asteraceae: Inuleae) polyploid complex. Pl. Syst. Evol.

————. In press b. A phylogenetic reconstruction of *Antennaria* Gaertner (Asteraceae: Inuleae) Canad. J. Bot.

———— and G. L. STEBBINS. 1981. Chromosome numbers of North American species of *Antennaria* Gaertner (Asteraceae: Inuleae). Amer. J. Bot. 68:1342–1349.

———— and ————. 1983. Distribution of sexual and apomictic populations of *Antennaria parlinii*. Evolution 37:555–561.

———— and ————. 1987. Chromosome numbers, patterns of distribution, and apomixis in *Antennaria* (Asteraceae: Inuleae). Syst. Bot. 12:305–319.

CHMIELEWSKI, J. G. and C. C. CHINNAPPA. 1988. Taxonomic notes and chromosome numbers in *Antennaria* Gaertner (Asteraceae: Inuleae) from arctic North America. Arctic and Alpine Res. 20:117–124.

EVERT, E. F. 1984. A new species of *Antennaria* (Asteraceae) from Montana and Wyoming. Madroño 31:109–112.

HARTMAN, E. L. and M. L. ROTTMAN. 1988. The vegetation and alpine vascular flora of the Sawatch Range, Colorado. Madroño 35:202–225.

OSWALD, E. T. and J. P. SENYK. 1977. Ecoregions of Yukon Territory. Canadian Forestry Service, Pacific Forest Research Center, Victoria.

PACKER, J. G. and D. H. VITT. 1974. Mountain Park: a plant refugium in the Canadian Rocky Mountains. Canad. J. Bot. 52:1393–1409.

PORSILD, A. E. 1945. The alpine flora of the east slope of MacKenzie Mountains, Northwest Territories. Nat. Mus. Canad. Bull. 101, Ottawa.

————. 1950. The genus *Antennaria* in northwestern Canada. Canad. Field-Nat. 64:1–25.

———— and W. J. CODY. 1980. Vascular Plants of the Continental Northwest Territories. Nat. Mus. Canad., Ottawa.

PREST, V. K. 1984. The late Wisconsinan glacier complex. *In* R. J. Fulton (ed.), Quaternary stratigraphy of Canada—a Canadian contribution to IGCP project 24. Geological Survey of Canada paper 84-10, Ottawa.

ROHLF, F. J. 1987. NTSYS-pc: numerical taxonomy and multivariate analysis system for the IBM PC microcomputer (and compatibles). Applied Biostatistics, Inc., Setauket.

RUTTER, N. W. 1984. Pleistocene history of the western Canadian ice-free corridor. *In* R. J. Fulton (ed.), Quaternary stratigraphy of Canada—a Canadian contribution to IGCP project 24. Geological Survey of Canada paper 84-10, Ottawa.

WEBER, W. A. 1987. Colorado flora: western slope. Colorado Associated Univ. Press, Boulder.